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STUDIES ON THE FAMILY COELOPIDAE (DIPTERA)

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With 24 Text-figures

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Introduction

The Coelopidae are a small family of acalyptrate flies, the species of which breed in wrack beds on the shores of temperate and sub-arctic regions of both the Northern and Southern hemispheres. Five species occur in Britain. Their classification is as follows, synonyms being given in brackets.

Family Coelopidae (Phycodromidae)

1. *Oedoparea* (*Heteromyza*, *Heterochila*) *buccata* (Fallén).
2. *Orygma luctuosa* Meigen.
3. *Malacomyia* (*Phycodroma*, *Malacomyza*) *sciomyzina* (Haliday).
4. *Coelopa pilipes* Haliday (*frigida* Meigen).
5. *Coelopa* (*Fucomyia*) *frigida* (Fabricius) (*gravis*, *simplex*, *parvula* Haliday, *eximia* Stenhammar).

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This list differs from that given by Kloet and Hincks (1945). *Heterochila* is added as a synonym of *Oedoparea* to concur with various authors; *C. eximia* Stenhammar is given as a synonym of *C. frigida* (Fabricius) according to the thesis of Mayhew (1939); and *C. parvula* is also given as a synonym of *C. frigida* since the characters described by Haliday (1833) fall within the variation of structure now known to occur in the latter species.

The field work for the present study was carried out from October, 1955 to August, 1958, mainly at Whitburn, Co. Durham. A short description of the shore at Whitburn and the wrack beds found on it is given on p. 125.

Malacomyia sciomyzina was the only species of the five not encountered during the present study. This paper is concerned with *Coelopa frigida*, *C. pilipes*, *Orygma luctuosa* and *Oedoparea buccata*.

I. Systematics

(1) *The General Appearance of the Adults*

The diagnostic features of the family Coelopidae are given by Hennig (1937), by Séguy (1934) and, in less detail, by Colyer and Hammond (1951). The only detailed morphological investigation on the adults of the family is that of Mayhew (1939) on *Coelopa frigida* and *C. pilipes*. Hennig (*op. cit.*) gives short descriptions of the adults of these two species and also of *Malacomyia sciomyzina* and *Orygma luctuosa*. Unlike other dipterists (*e.g.* Oldroyd (1954) and Séguy (*op. cit.*)) he does not consider *Orygma luctuosa* or *Oedoparea buccata* to be species of Coelopidae, although he deals with *O. luctuosa* in his paper on that family. *Oe. buccata* (as *Heterochila buccata*) is described briefly by Czerny in his work on the Dryomyzidae (1930). Séguy (*op. cit.*) gives the distinguishing features of each of the genera and species and includes a key to their identification which is suitable for students in the British Isles.

It is necessary here to give only an indication of the appearance of the flies and to mention the variation in size that was found in wild specimens.

Coelopa frigida, which is a very bristly, dorsoventrally flattened black fly, is the most variable of the Coelopids in size and appearance. Males measured between 3 mm. and 9 mm. in length (from the front of the head between the antennae to the tip of the abdomen) and females between 3 mm. and 7 mm. Mayhew (*op. cit.*) showed that the larger flies had proportionately longer bristles, thus giving them a different appearance, which probably accounts for the several synonyms used for this species.

C. pilipes closely resembles *C. frigida*, but, instead of being bristly, it is covered with a fur of fine hairs. The females are most alike, but can be distinguished by their tibiae. The tibia of *C. frigida* bears a preapical bristle, which in *C. pilipes* is only slightly developed and is obscured by dense hairs. *C. pilipes* is less variable in size, specimens measuring between 4·5 and 7·5 mm.

Orygma luctuosa is also a black, dorsoventrally flattened fly but it is not so hairy and bristly as the two species of *Coelopa*. It is more constant in size, males measuring 5·5–6·75 mm. and females 4·75–6·0 mm. long. It differs, too, in having a few long hairs on its metathoracic spiracles.

Oedoparea buccata is a light brown to orange-coloured fly with a grey thoracic region and it is a little less flattened, dorsoventrally, than the other three species. Male specimens ranged from 4·5 to 7·5 mm. long (less than one-fifth were under 6·5 mm.) and females from 4·5 to 6·0 mm. In May, 1957, however, a small group of this species was caught, all of which were only 3·5 mm. long and had the abdomen grey as well as the thorax.

The males of each of the species are in general more hairy or bristly than the females, but the bristles used for purposes of classification in the Diptera are usually

more developed in the females and more distinct, since they are not so obscured by the general covering of bristles and hairs present in the males.

(2) *The Young Stages*

The young stages of each of these four species consist of the egg, three larval instars and a pupa which is contained within a puparium.

The only detailed account of the external structure of these stages was given by Mayhew (1939) and concerned only *C. frigida* and *C. pilipes*, though he failed to find any real distinguishing features between them. A less detailed study of the stages of *C. frigida* was made by Elwes (1915), and brief descriptions of the mature larva and puparium were given by Hennig. The young stages of the other two species have received only little attention. Backlund (1945*b*) gave a brief account of the third instar larva and puparium of *Oedoparea buccata*, and the only useful information available on *Orygma luctuosa* is the short description of a damaged puparium by Scott (1920).

Concerning *C. frigida*, it is sufficient here to describe only its third instar larva and puparium so that they may be compared with those of the other species of Coelopidae. This will be followed by a discussion of the features that distinguish the larvae and puparia of *C. pilipes* and *C. frigida*, and a detailed account of the young stages of *O. luctuosa* and *Oe. buccata*.

(3) *The Larva and Puparium of* Coelopa frigida (*Fabricius*)

The following account of the structure of the third instar larva of *C. frigida* is based on the thesis of Mayhew (1939). Further details have been added, particularly concerning the structures which differ from those found in the other genera of the family.

Third Instar Larva

Length 5·0–13·75 mm., when food plentiful 10·0–13·75 mm.; breadth 1·6–1·8 mm. at widest point, greatest depth 1·7–1·9 mm. *Shape* cylindrical, anterior third tapering to head; blunt posteriorly. *Colour* white, except for brown to black sclerotised regions. *Body* of the normal 12 segments; first segment indicated dorsally by the projecting antennae, segments 3–11 subequal in length (*c.* 1 mm.), 2 shorter and 12 only about half their length. *First segment* of 2 lobes separated by a median ventral groove, at posterior end of which is mouth; bears in front, one on each lobe, a pair of small, forwardly-directed, 2-segmented antennae; posterior to these, on antero-ventral margin of each lobe, are the pair of " maxillary palps ", each appearing to consist of a sclerotised ring surrounding a central transparent segment. A third pair of sensory organs, the smallest (just visible at × 100), one on each lobe, lateral to anterior margin of grooves in which bifurcate mouth-hooks are situated; each lobe with a number of rows of sclerotised teeth; at sides of mouth-hooks 3 rows of 9–10 teeth present, stretching right along ventral surface; anterior to mouth-hooks a further 2 distinct rows of 12–15 teeth, and anterior to these the teeth present in less distinct and gradually shortening rows to a point level with maxillary palps; teeth diminish in size anteriorly and laterally, so that the largest occur immediately to side and front of mouth-hooks. *Anterior spiracles* situated laterally near posterior margin of second segment; each composed of 13–19 digitate processes, at tip of which are the spiracular openings. *Posterior spiracles* borne on backwardly-directed projections from dorsal part of segment 12; peritreme dark brown and roughly kidney-shaped, the convex side directed outwards; a ring, broken in region of cicatrix, of about 50 branched processes arises from inside peritreme; each process broad and thin proximally but becoming more hair-like distally; 3 roughly semicircular, spiracular slits present, each closed by a fine sclerotised grating. *Spines*: ventral surface slightly swollen at margins of each of segments 3–12; the swellings running transversely across larva and bearing about 12 broken rows of small spines; those on segments 2, 3 and 4 smaller than those on more posterior segments, whilst in each group of rows the more anterior spines slightly smaller than the posterior; the anterior (*c.* 9) rows of each group usually curved forwards, posterior (*c.* 3) rows

being curved backwards ; anal lobe with spines in rough circles, pointing outwards ; these ventral groups of spines extend round anterior margin of segments 3–5, whilst traces of them are found dorsally on anterior margins of segments 6, 7 and 8. *Anus* opens on ventral lobe of last (twelfth) segment and consists of a longitudinal slit dividing lobe into 2 lateral and one anterior portions ; 3 large sclerotised processes each composed of 4–10 spines at end of anus.

Puparium

Length, from full grown larva, *c.* 7·5 mm. Dark brown to black ; outline ovate, tapering anteriorly, posterior end blunt ; in side view ventral line straight, sometimes very gently sinuous ; dorsal line convex, tapering anteriorly, deepest in region of segments 8–9 ; first segment completely introverted, so that larval anterior spiracles are situated almost at anterior end of puparium ; split occurs laterally round anterior end to allow emergence of adult, part of puparium dorsal to split breaking off transversely three-quarters way along segment 4, usually leaving ventral part intact.

Remarks.—It is difficult to decide whether the antennae of the larva of *C. frigida* and the other species of Coelopidae described in this paper are two-segmented and placed on a projection of the head lobes or whether they are three-segmented, the projections of the head lobes being in fact third segments. They are described here as being two-segmented.

(4) *Differences between the Larvae of* Coelopa frigida *and* C. pilipes *Haliday*

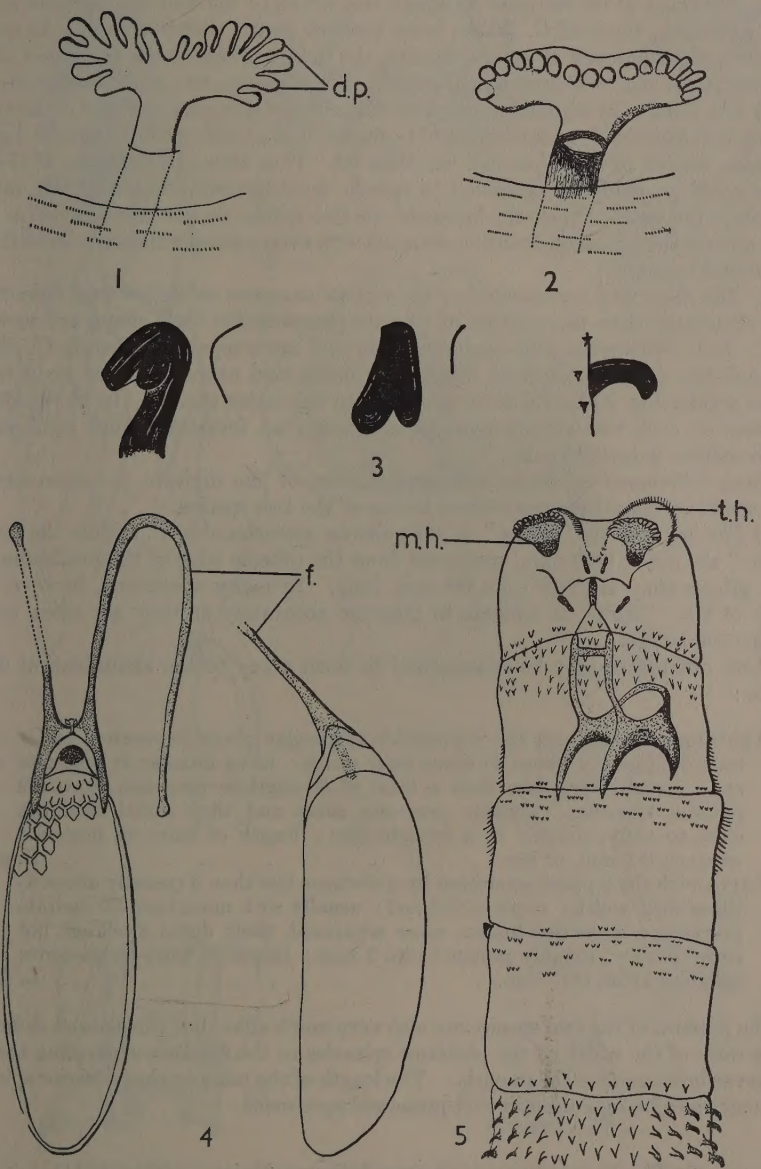
The above description of the larva of *C. frigida* could also apply to that of *C. pilipes*, the differences being only slight. The differences given by Hennig (1937) are not genuine and the use of his key to the identification of *Coelopa* larvae could often lead to error.

To determine the difference between the larvae of the two species, each was bred under similar conditions (p. 120) at the same time of the year (August and September, 1957). All the larvae were supplied with adequate food (*Laminaria* stipes) and etherised after one or two had begun to pupate. When killed, parts of the larvae, particularly the sides between segments 5–11, the digitate processes of the anterior spiracles and the rim of the posterior spiracles, turned black (*i.e.* the cuticle became tanned) within a few minutes. Each larva was extended to full length by being gently pressed between the thumb and first finger. The specimens examined were therefore freshly-killed, mature third instar larvae in the fully extended position.

Measurements of 50 specimens of each of the two species were noted, and are summarised below. Measurements *a*, *b*, *c*, *d* and *e* are in mm., *b*, *c*, *d* and *e* being taken with a micrometer eyepiece at a magnification of $\times 16$.

		C. frigida		*C. pilipes*	
		mean	s.d.	mean	s.d.
a	Length	12·03	0·66	13·03	0·45
b	Width of last segment	2·58	.	3·21	.
c	Shortest distance between posterior spiracles	0·86	.	1·34	.
d	Distance between outside edges of posterior spiracles	1·66	.	2·00	.
e	Width of spiracular plate, which is equal to $\frac{(d)-(c)}{2}$	0·40	.	0·33	.
	$\frac{c}{e}$	2·14	0·10	4·00	0·23
	Number of digitate processes on anterior spiracles	32·2	.	28·3	.

(a) *The ratio of the width of one of the spiracular plates to the distance between them.*—It will be seen that in *C. frigida* the two spiracular plates of the larvae were separated by a distance of about twice their width, whilst those of *C. pilipes* were separated by about four times their width. This difference became noticeable as soon as the



FIGS. 1–5.—(1) *Coelopa frigida*, larva, anterior spiracle; (2) *C. pilipes*, larva, anterior spiracle; (3) *C. frigida*, mouth hooks, ventral, anterior and lateral views; (4) *Orygma luctuosa*, egg, ventral and lateral views; (5) the same, first instar larva, ventral view. (*d.p.*, digitate processes; *f.* filaments; *m.h.*, mouth hooks; *t.h.* transparent hood.)

measurements were taken, and was used later as the easiest and surest way of identifying wild third instar larvae of these two species.

(b) *The shape of the larvae.*—Although the larvae of the two species were almost equal in length, those of *C. pilipes* were broader at the posterior end. As can be seen from the summary of measurements, the last segment of the *C. pilipes* larvae was over 20 per cent. wider than in *C. frigida*. This feature, too, soon became obvious.

(c) *The number of digitate processes on the anterior spiracles.*—Of the 50 larvae of each species examined, 44 specimens of *C. frigida* had a total of more than 30 digitate processes, and 41 of *C. pilipes* had less than 30. Thus about 80 per cent. of *Coelopa* larvae could probably be identified to specific level by examination of the number of digitate processes. Since the larvae of the two species do not intermingle (p. 130), fairly certain identification could be obtained with even a small number, provided they were found together.

(d) *The shape and arrangement of the digitate processes on the anterior spiracles.*—More significant than the number of digitate processes are their shape and arrangement. In *C. frigida* the processes are longer and more separated than in *C. pilipes*, the knob-like swellings at their distal ends being held away from the body in the former species (fig. 1) but close to the body in the latter (fig. 2). In *C. frigida* the processes on each side are arranged in two rough fan formations, but in *C. pilipes* this formation is less obvious.

These differences in shape and arrangement of the digitate processes are the most useful for identifying preserved larvae of the two species.

(e) *The length of the "hairs" on the posterior spiracles.*—In *C. frigida* the longest "hairs" are about 0·15 mm., measured from the outside edge of the peritreme, and in *C. pilipes* they are less than 0·1 mm. long. In many specimens, however, the length of the "hairs" is difficult to measure accurately as they are often curved towards the larvae.

These differences may be summarised to form a key to the identification of the species :

Third instar larva with the 2 posterior spiracular plates separated by at least 3·5 (usually about 4) times their width ; larva broader at posterior end ; usually with less than a total of 30 digitate processes on the 2 anterior spiracles ; digitate processes short and their distal swellings close to body, roughly in a straight line ; length of hairs on posterior spiracles 0·1 mm. or less . . . . . **C. pilipes**

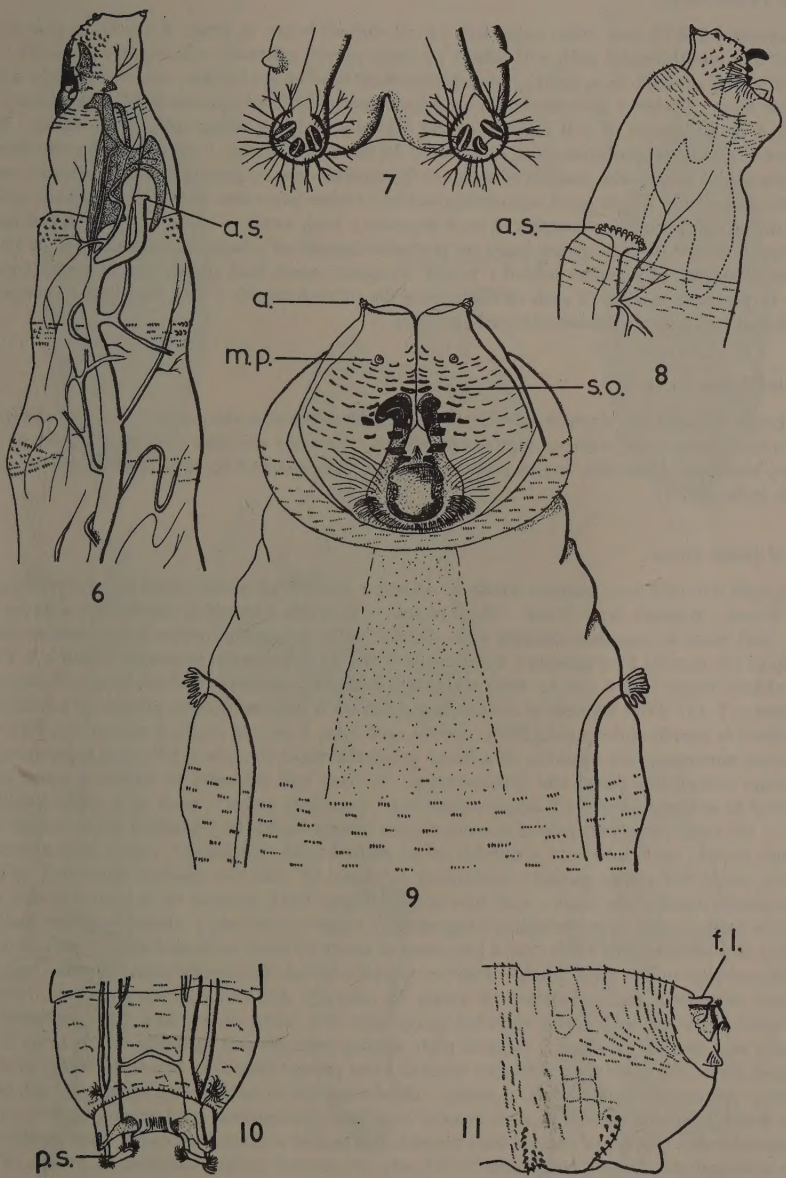
Larva with the 2 plates separated by a distance less than 3 (usually about 2) times their width ; more cylindrical ; usually with more than 30 digitate processes ; processes longer, more separated, their distal swellings not close to body, roughly grouped into 2 fans ; length of hairs on posterior spiracles about 0·15 mm. . . . . **C. frigida**

The puparia of the two species are also very much alike, but the distinct difference in the ratio of the width of the posterior spiracles to the distance separating them in the larvae holds good in the puparia. The length of the hairs on the posterior spiracles can sometimes be measured in well-preserved specimens.

(5) *The Young Stages of* Orygma luctuosa *Meigen.* (Figs. 4–14)

Egg

Length 0·8 mm.; in dorsal view elongate-ovate ; in side view dorsal surface convex, ventral surface almost straight. Two long (1 mm.) thin, white filaments attached to anterior end ; the filaments cylindrical, slightly narrowing near distal end before gently swelling into a small bulb ; a small funnel-shaped structure present between filaments at anterior extremity through which a fine passage (micropyle) leads into egg ; colour white ; whole chorion covered in white reticulation of hexagons of roughly equal size, except for some smaller ones at anterior end on ventral side.



FIGS. 6–11.—*Orygma luctuosa* : (6) second instar larva, anterior end, lateral view ; (7) posterior spiracles ; (8–11) third instar larva ; (8) anterior end, lateral view ; (9) anterior end, ventral view ; (10) posterior end, dorsal view ; (11) posterior end, lateral view. (*a.*, antennae ; *a.s.*, anterior spiracle ; *f.l.*, fleshy lobe ; *m.p.*, " maxillary palp " ; *p.s.*, posterior spiracle ; *s.o.*, third pair of sensory organs.)

First Instar Larva

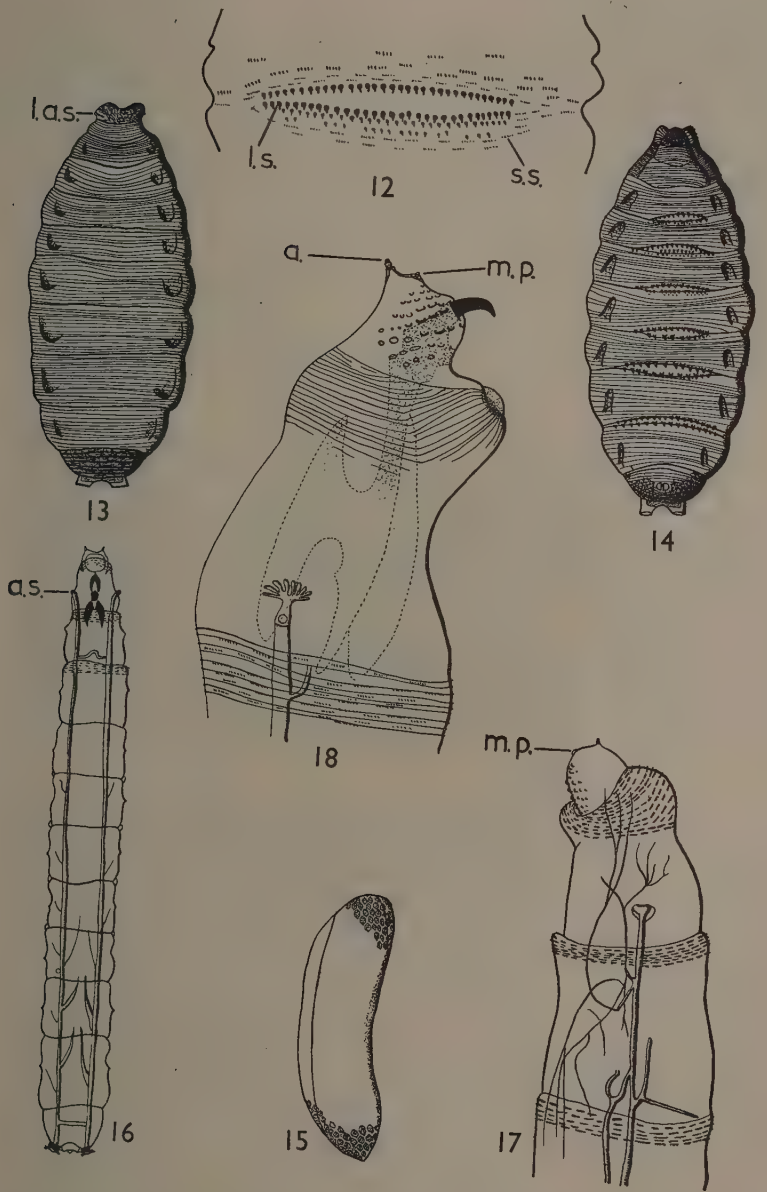
Length 1·5–3·25 mm. when extended. *First segment* bears, in front of mouth, a pair of large comb-like mouth-hooks, each with about 20 teeth curved ventrally and slightly inwardly; each mouth-hook covered by a hood of transparent skin bearing on its free, anterior margin a fringe of fine hairs. *Posterior spiracles* borne on 2 backwardly-directed processes of last segment; each with 4 rough groups of 3–6 hairs, directed laterally or lying along sides of processes. *Spines* present in marginal positions on all segments 2–12 on ventral surface; small, backwardly-directed, simple spines on anterior margin of segment 2; smaller ones in groups of 3–5 at anterior margin of segments 3 and 4; those on segments posterior to these larger and borne on transverse swellings at anterior and posterior margins of each segment; each swelling bears a group of 4–6 rows of spines, first row of each group being at posterior margin of a segment and the others towards anterior margin of segment behind; nearly all spines curve backwards, but those in the single row at posterior margin of each of segments 8–10 curve forwards; fine, hair-like spines present on dorsal and lateral surfaces of segments 2–12.

Second Instar Larva

Length 2·75–6 mm. *Anterior spiracles* situated laterally near posterior border of second segment; knob-like, fan-shaped, without digitate processes. *Posterior spiracles* each with circlet of 25–30 hairs, nearly all branched, round peritreme; each hair one-half to two-thirds width of stigmal plate in length.

Third Instar Larva

Length 6·0–16·0 mm., mature larvae 14–16 mm.; breadth at widest point (in region of segment 9) 1·8 mm.; greatest depth 2 mm. *Shape* almost cylindrical, narrowing slightly towards posterior end, and more so towards anterior end. *Colour* white except for brown sclerotised structures. *Body* of the normal 12 segments; segments 3–7 and 12 subequal in length (*c.* 1 mm.), 8–11 subequal and longer (*c.* 1·6 mm.); each segment 3–6 slightly concave on dorsal surface, straight in segments 7–11. *First segment* of 2 lobes separated by a median ventral groove at posterior end of which is mouth and bears in front, one on each lobe, a pair of small, 2-segmented, forwardly-directed antennae, each situated on a fleshy projection from the lobe; proximal segment of each antenna cylindrical, distal one hemispherical, its base half diameter of former; posterior and ventral to antennae are the 2 single-segmented " maxillary palps ", each on a slight swelling of lobe; the third (smallest) pair of sensory organs clearly visible in a position anterolateral to the mouth-hooks; each lobe with a number of sclerotised teeth, the largest, placed near the mouth-hooks, being flat plates pointing backwards at about 45° and the smallest appearing as brown sclerotised ridges in the lobes; each lobe with 1–2 large teeth anterior to its mouth-hook; about 4 large teeth lateral to it, becoming progressively larger posteriorly; about 5 smaller teeth in a row at side of each large tooth, and 2 long rows of about 10 small teeth and 4 short rows of 4 small teeth anterior to the large teeth. *Anterior spiracles* situated laterally near posterior margin of second segment; each composed of about 15 laterally directed digitate processes. *Posterior spiracles* borne on backwardly-directed projections (0·4 mm.) of segment 12; peritreme light brown and circular in shape; stigmal plate sloping inwards and upwards and bearing 3 arch-shaped spiracular openings; 3 fringes of small hairs present (less than one-third width of stigmal plate), each opposite a spiracular opening; closely applied to laterodorsal surface of each process is a fleshy lobe and ventral to each process is a fleshy transparent cone-shaped papilla pointing ventrolaterally. *Spines* of various sizes present, but largest and smallest easily distinguished from the intermediate; largest single and found only on ventral surface, smallest in groups of 2–12. Individual larvae vary slightly but are similar to following; segments 2, 3 and 4 bear a number of rows of small spines in groups which extend right round segment at its anterior margin; segment 5 has 6–7 rows of small spines, the more posterior rows extending round dorsal surface; segments posterior to these bear spines arranged as shown in diagram for segment 8 (fig. 12); all segments with 2 rows of large spines, the number of spines in each decreasing posteriorly from about 33 in segments 6–8 to about 19 in segment 12; 2–3 rows of groups of small spines present anteriorly and posteriorly to the large spines. *Anus* opens at posterior end of segment 12; lateral to it are 2 roughly triangular-shaped (in side view), fleshy lobes bearing small spines on their margin and outer surface.



FIGS. 12–18.—(12–14) *Orygma luctuosa*: (12) third instar larva, spines on segment 8; (13) puparium, dorsal view; (14) the same, ventral view. (15–18) *Oedoparea buccata*: (15) egg; (16) second instar larva, dorsal view; (17) the same, anterior end, lateral view; (18) third instar larva, anterior end, lateral view. (*a.*, antennae; *a.s.*, anterior spiracles; *l.a.s.*, larval anterior spiracle; *l.s.*, large spine; *m.p.*, " maxillary palp "; *s.s.*, group of small spines.)

Puparium

Length 7·0–7·5 mm., greatest width 3·5–4 mm., greatest depth (at segment 8) 3·0–3·3 mm. *Colour* black except for anterior 2 segments and posterior spiracles which are brown; surface dull. Outline elongate ovate, with segments 6–10 of roughly equal width, tapering, anteriorly and posteriorly to these, to about one-third to one-quarter greatest width; in side view ventral line slopes down to segment 6 and continues straight to middle of segment 12, where it quickly rises to posterior respiratory processes; dorsal line convex, tapering at anterior end. *Segmentation* clearly defined, constrictions being between segments and larval segmental spines obvious; first segment completely introverted so that larval anterior spiracles are situated only short distance from anterior end; skin in ridges which extend right round body, about 20 to each segment; shallow longitudinal cavities towards lateral margins of each of segments 5–11, one dorsal and one ventral on each side, each rising slightly from anterior to posterior margin of segment. Puparium covered in white calcareous layer (can be dissolved in weak acid for examination of puparium); thickest all over first 3 or 4 and last segments and between segments on ventral surface, present to less extent between segments on dorsal surface. To allow emergence of adult, puparium splits half-way along segment 5 and then laterally right round anterior end, the two parts so formed being either pushed apart or broken off.

(6) *The Young Stages of* Oedoparea buccata (*Fallén*). (Figs. 15–23)

Egg

Length 0·8 mm.; in dorsal view elongate ovate; in side view dorsal surface convex, ventral surface concave; anterior end more tapered than the other, which is more rounded; colour white; whole surface of chorion covered with sculptured hexagons of roughly equal size.

Second Instar Larva

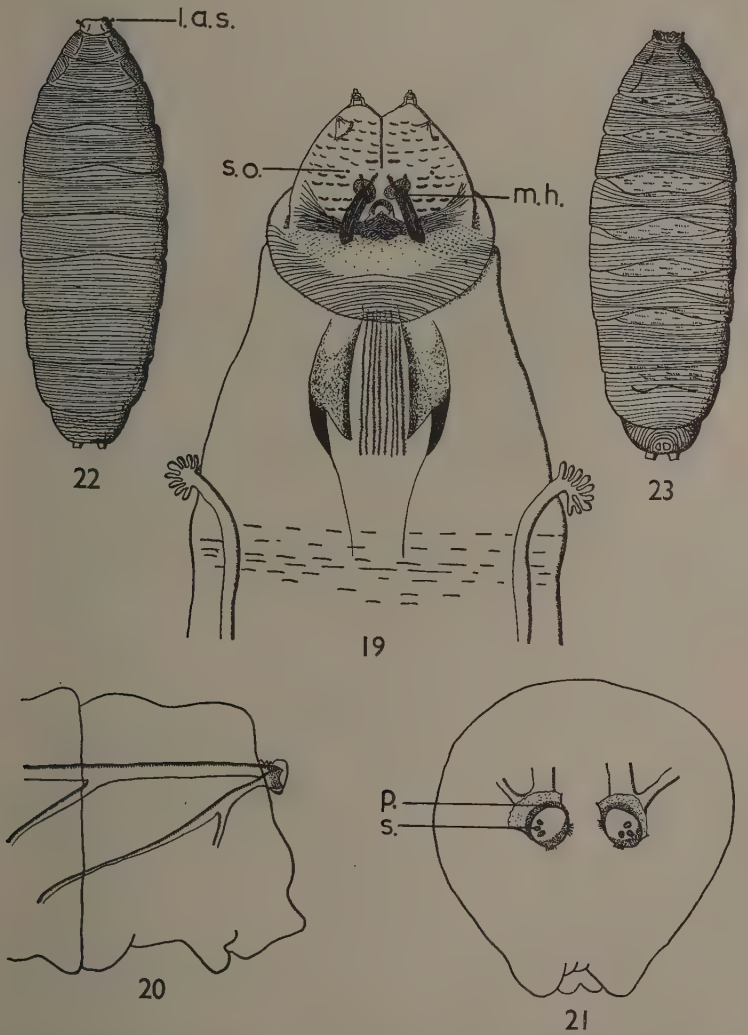
Length 2·5–4·5 mm. *Anterior spiracles* situated on second segment near posterior margin in a lateral position; each a small knob-like structure, projecting from larva laterally, surrounded by a flap of transparent skin; without digitate processes. *Posterior spiracles* on backwardly-directed processes of segment 12; peritreme black to dark-brown, with small hairs in 3 groups—one lateral, one dorsolateral and one ventrolateral.

Third Instar Larva

Length 4·5–10 mm.; when food plentiful 9–10 mm.; greatest width (in region of segment 8) 1·5 mm.; greatest depth 1·5 mm. *Shape* almost cylindrical, narrowing only very slightly posterior to segment 9, more so anterior to segment 5. *Colour* white except for brown sclerotised structures. *Body* of the normal 12 segments; 3–8 subequal in length, 9–11 subequal and longer; all segments clearly indicated ventrally by swellings at both anterior and posterior margins of segments 2–11 and at anterior margin of 12; not so clearly indicated dorsally, as marginal swellings are gentle; slight rise in middle of each of segments 3–11. *First segment* of 2 lobes separated by a median ventral groove at posterior end of which is mouth, and bears, in front, one on each lobe, a pair of small, 2-segmented, forwardly-directed antennae, each situated on a fleshy projection from the lobe; proximal segment of each antenna almost cylindrical, only very slightly tapering to base; distal segment hemispherical; posterior and ventral to antennae are, one on a swelling of each lobe, the single-segmented "maxillary palps"; a third pair of sensory organs (the smallest), situated anterolaterally to grooves in which mouth-hooks are found; each lobe with 5 rows of sclerotised teeth at sides of mouth-hooks, 3–6 teeth in each row, and about 5 rows anterior to mouth-hooks; teeth diminish in size anteriorly and laterally so that largest teeth are found nearest to mouth-hooks. *Anterior spiracles* situated laterally near posterior margin of second segment; each composed of 7–10 digitate processes. *Posterior spiracles* borne on backwardly-directed projections of segment 12; peritreme light brown and roughly circular; stigmal plate with 3 roughly oval spiracular openings and 2 or 3 groups of very small, fine hairs, set at right angles to length of body. *Spines:* rows of groups of very small backwardly-directed spines on ventral surface at margins of segments 3 or 4 to 12; white to very light brown in colour. *Anus* opens towards end of twelfth (last) segment; surrounded by 4 fused lobes, 2 (the largest) at the sides, one in front, and the fourth (the smallest) behind; front lobe saddle-shaped, giving appearance of 2 lobes; some very small spines present on inside face of posterior lobe.

Puparium

Length from full grown larva, 6·5–7 mm.; greatest depth (in region of segment 8) 1·6–1·8 mm.; greatest width 1·6–1·8 mm. *Colour:* light to dark brown with black lines between each segment on dorsal surface and (larval) posterior respiratory spiracles light brown; surface shining. Outline more cylindrical than ovate, tapering posteriorly and anteriorly to about one-third greatest width; in side view ventral line slopes down to segment 6 and continues straight to segment 11, where it rises slightly to end of segment 12; dorsal line convex, tapering at anterior end. *Segmentation* not clearly defined but usually with a black edge to each segment on dorsal surface. First segment completely introverted, so that larval anterior spiracles are situated only a short distance from anterior end; skin in fine transverse ridges, each extending right



FIGS. 19–23.—*Oedoparea buccata*: (19–21) third instar larva: (19) anterior end, ventral view: (20) posterior end, lateral view; (21) posterior end, posterior view; (22–23) puparium: (22) dorsal view; (23) ventral view. (*l.a.s.*, larval anterior spiracle; *m.h.*, mouth hooks: *p.*, peritreme; *s.*, spiracular opening; *s.o.*, third pair of sensory organs.)

round puparium ; segments 3, 4 and 5 with entire skin ridged ; 6–10 inclusive with ridges (between 10 and 15 per segment) towards centre of each segment ; on 11 and 12 all surface thrown into ridges. To allow emergence of adult, splits occur laterally round anterior end, and round sides at posterior margin of segment 4, thus forming a dorsal and ventral flap ; the emerging fly forces one or the other open leaving the opposite flap more or less intact.

(7) *The Systematic Position of* Oedoparea buccata

Some little doubt seems to exist regarding the systematic position of *Oe. buccata*, most dipterists placing it in the family Coelopidae, but Hennig (1937) excludes it from this family and considers it a species of Dryomyzidae. Fortunately, I was able to study a species of wrack-breeding fly, *Helcomyza ustulata* Curtis, which undoubtedly belongs in the Dryomyzidae and can, therefore, be used to indicate the morphological features present in species of that family.

Backlund (1945*b*) briefly compared the third instar larva of *Oe. buccata* with a description, by Gadeau de Kerville (1894), of the supposed larva of *H. ustulata*, and came to the conclusion that the larva of *Oe. buccata* was so different from that of *H. ustulata* that the two species could not possibly belong to the same family. Since Gadeau de Kerville did not rear adults from the larvae he described, there was some doubt about their identification, and Backlund's conclusions could not go beyond this. At this stage the larva described by Gadeau de Kerville need not have been that of a species of Dryomyzidae, in which case *Oe. buccata* could be a member of that family.

H. ustulata occurs at Whitburn and its larvae, which have been found in the wrack beds there, have been reared through to the adult stage. This has shown that the larva described by Gadeau de Kerville was not that of *H. ustulata*, the true larva of which will be described elsewhere. However, the larva of *Oe. buccata* is at least as different from the true larva of *H. ustulata* as it is from the larva described by Gadeau de Kerville, and Backlund's conclusion that these two species must belong to different families remains valid. *Oe. buccata* cannot, therefore, possibly be a species of Dryomyzidae.

As can be seen from the descriptions and figures provided, the larva of *Oe. buccata* differs considerably from that of the species of *Coelopa*, but this could still be merely an intrafamilial difference. There seems no reason why *Oe. buccata* should not remain a member of the family Coelopidae, at least until further knowledge of the affinities of acalyptrate flies shows otherwise.

II. Laboratory Cultures and Observations

Cultures of the four species of Coelopidae were maintained in jars containing split *Laminaria* stipes in a manner similar to that described for culturing *C. frigida* by Mayhew (1939) and Thompson (1951). For her genetical work Thompson found it most convenient to use small milk bottles stoppered with a plug of cotton wool. The present writer used 2–lb. size Kilner jars, the glass lids of which were replaced by circular pieces of perforated cardboard.

To prevent the split *Laminaria* stipes from drying up and withering they were placed on wet sand or cellulose wool. If there were no larvae feeding in the culture, the *Laminaria* often became mouldy or covered in a thick opaque slime within a few days. Since eggs were not normally laid on weed in either of these conditions, it was either scraped and washed free of slime and mould or replaced by fresh weed. While larvae were feeding, neither the mould nor the opaque slime developed ; instead the weed decomposed quickly, a brown semifluid running from it. If this became too deep it was removed with a pipette to prevent the larvae from drowning.

Firm *Laminaria* stipes were collected from temporary wrack beds formed below

the high-tide level and free of animal life other than small nematodes, which were usually present. The stipes were washed and examined in the laboratory to avoid the accidental introduction of other animals or their eggs into the cultures, but no attempt was made to free the *Laminaria* of the nematodes, as they helped in the initial breakdown of the wrack tissues and, when present in large numbers, prevented the formation of moulds.

Because the wrack beds were visited frequently there was never any need to store *Laminaria* stipes for more than a day or two. If storage for longer periods is required it should be tightly packed in screw-top jars and kept in a cool, dark place (Thompson, 1951).

The cultures were kept at room temperature on a bench in the laboratory or in a room with a controlled temperature of 24° C.

(1) *Coelopa frigida* (Fabricius)

Under the conditions described above most of the female flies eventually laid eggs. Usually one or two batches of between 60 and 80 eggs were laid, but two females each laid a third batch. The eggs in a batch hatched within a few minutes of each other, and the young larvae made their way into the soft *Laminaria* tissue. Here they could be found while in their first and sometimes their second instars, their bodies immersed in the soft wrack and only their posterior spiracles visible. The third instar larvae were found both on and in the *Laminaria* stipes and wandering over the inside of the jar. They pupated in clusters in the upper, drier parts of the jar or on the top of the remaining stipes.

Thompson (1951), who bred a large number of samples, found that at 24° C. the time from egg laying to the emergence of the adult was between 11 and 12 days.

(2) *Coelopa pilipes* Haliday

Unlike *C. frigida*, females of *C. pilipes* were very reluctant to lay eggs in the conditions described. In 53 jars, each containing one to four females and several males, set up at various times throughout the period during which the flies were found in the field, only five batches of eggs were laid, all on the outside surface of the *Laminaria* stipes. The resulting larvae, however, thrived in much the same way as *C. frigida*, and those not killed and preserved eventually pupated in clusters in the same way.

At room temperature the total time from the laying of the egg until the emergence of the adult was from 17 to 25 days. Various conditions differing from those described above in the amount of water in the culture jar, the state of decomposition of the wrack and the kind of wrack offered (i.e. *Fucus* instead of *Laminaria*) were found to be no more suitable for egg-laying. Since *C. pilipes* was being cultured chiefly to procure examples of its young stages for comparison with those of *C. frigida*, and adequate material had been obtained for this purpose, no further attempts were made to find better egg-laying conditions.

(3) *Orygma luctuosa* Meigen

Since the eggs of *O. luctuosa* were embedded in the wrack tissue, the most suitable *Laminaria* stipes for egg-laying were those which were soft but firm. Wrack in this state was quickly obtained by adding several nematodes of the species normally found in the wrack beds to the split *Laminaria* stipes in the culture jars set up for this Coelopid. The nematodes reproduced very quickly and their activities soon softened the top 2 or 3 mm. of the cut surface of the stipes. If the flies were newly emerged they were placed with the *Laminaria* fresh from the wrack beds—the eggs in the female ripened whilst the surface layers of the weed were being softened. In the

wild the larvae pupate in compressed wrack material and in the laboratory it was found that a layer of tightly-packed, moist cellulose wool placed in the bottom of the jar after all excess water had been removed was a suitable substitute.

Isolated pairs of flies in the culture jars mated frequently and at all times of the day. The flies were together for up to 15 minutes, the female walking round the jar with the male in the copulatory position, but actual union lasted only three or four minutes. Males often tried to mate with etherised and immobile females.

The first eggs of each female were laid one to five days after copulation, this variation being probably due to the different state of decomposition of the *Laminara* provided. The frequent matings of the females are apparently not necessary for the production of fertile eggs, as four of six bred females, which were allowed to mate only once, laid fertile eggs, the other two dying without laying eggs after only a short life.

Up to about 180 eggs were laid by each female (nine bred flies laid 41, 63, 83, 89, 96, 113, 151, 178 and 179 eggs respectively) within 12 hours. Each egg was embedded in the soft tissue of the cut surface of the *Laminaria* stipe, with its two long filaments either projecting into the air or lying along the wrack surface. A few eggs were sometimes laid amongst the wet cellulose wool, but none was ever laid on the surface of hard *Laminaria* stipes. The eggs were laid 2–3 mm. apart, only their filaments occasionally touching. The filaments have a respiratory, and not just the mechanical function of preventing the egg from sinking into the soft wrack tissue; eggs the filaments of which had been gently pushed just below the surface of the wrack, or those in which the filaments had been severed at their base, failed to hatch.

The eggs hatched in one to two days.

After hatching, the first instar larvae buried themselves in the soft wrack tissue, their posterior spiracles with their circlet of hairs only remaining in view. The second instar larvae sometimes fed in this position, but more usually on the surface of the wrack. The third instar larvae fed on the surface and were the only ones found away from the *Laminaria* stipes, on the lid or side of the jar.

In June at room temperature both the first and second instar stages each lasted two to three days, but the length of the third instar stage varied considerably, some larvae feeding up quickly and pupating in ten days, others being found still on the wrack or wandering round the jar up to six weeks later. This was probably because the larvae did not find suitable places in which to pupate. At room temperature in winter the larvae were very lethargic and the stages lasted much longer, six to eight days for each of the first and second instar stages and ten to twelve weeks for that of the third instar.

The larvae pupated singly in either the moist, tightly-packed cellulose wool placed at the bottom of the jar for this purpose, or inside pieces of moist wrack material. Pupae were never found lying either on or under the cellulose wool or in wet weed. The larvae contract after entering the material; thus a small chamber is produced, the puparia remaining in contact with the wrack on their ventral surface only.

The pupal stage lasted from eight to thirteen days at room temperature in May, but larvae that pupated on 13th and 14th November, 1956, did not give adults until 20th–26th March, 1957, *i.e.* 19 weeks later. This coincides with the cessation of activity that is observed in the field at this stage in the life-history.

(4) *Oedoparea buccata* (Fallén)

As will be shown later in this account, larvae of *Oe. buccata* did not survive well under wet conditions and, since they normally pupated under material at the bottom of the jar, the jar had to be well drained. For this purpose sand was found more suitable than cellulose wool; more could easily be added if that at the bottom of the

jar became too wet, it was the natural pupating medium, and pupae in it could easily be removed. All excess water and semifluid lying on the sand was removed with a pipette.

Coition of isolated pairs of flies occurred frequently and at all times of the day. The male jumped on to the female from behind and gripped her round the abdomen with his metathoracic legs. The genital complex of the male was extended and union effected. The females were often walking round the jar with the male in the copulatory position for periods up to half an hour, but actual union seemed to last less than two minutes.

Eggs were laid one to three days after the first act of copulation had been observed. Over the next few days, up to 200 eggs were laid singly or in small groups of up to about 15, the eggs often just touching but never overlapping. Most were laid with the dorsal convex surface uppermost, but occasionally they were laid on their side or with the ventral surface uppermost.

The state of the *Laminaria* stipes undoubtedly affects oviposition greatly, *Oe. buccata* being a much more selective fly than *C. frigida*. Of 1532 eggs laid by 17 females of *Oe. buccata*, 1481 were found on the outside surface of the split *Laminaria* stipes amongst various branched epiphytes, *etc.* that grew on it or near the margins of the cut surface (*i.e.* on the assimilating layer), and only 51 were found on the more central tissue of the cut surface. They were always found on moist areas of the stipes, but not where a film of water was present. Eggs of *Oe. buccata* were never laid anywhere other than on the *Laminaria* stipes provided. Females of *C. frigida*, however, have laid their eggs on *Laminaria* in all states of decomposition and on a few occasions on damp corks and on moist parts of the side of the jar.

The shells of the eggs of *Oe. buccata* were very sticky when damp, and they were difficult to dislodge after the moisture round them had dried.

The first instar larvae either fed on the outside of the *Laminaria* stipes or buried themselves in the soft tissue, leaving only their posterior spiracles in direct contact with the air. The older larvae usually fed on the outside of the weed, making inroads into the more central tissue or on the harder parts of the cut surface.

The first instar stage lasted three to four days and that of the second instar four to five days when the cultures were kept at room temperature, but great variation was found in the length of the third instar stage. The third instar larvae fed well and were active for about four weeks, but they then became very lethargic, remaining in small groups under the sand or under weed lying on it, and ate very little. This continued for five to six weeks, when they eventually pupated. The period from the hatching of the egg until the resulting larvae pupated lasted about ten weeks at room temperature and six weeks at 24° C.

The larvae pupated in the sand at the bottom of the jar provided it was only damp and not waterlogged, in which case they wandered round the jar for several days, sometimes weeks, and usually died, although a small number sometimes managed to pupate on the drier parts of the *Laminaria* stipes or on the side of the jar. At the time for pupation the larvae were found together and often pupated in contact with one another, but they never formed masses of adhering pupae as in *C. frigida*. Most larvae of the same age pupated within a day or two of each other, but there were usually some in each culture which did not pupate until up to 15 days later. It took two to three days for the puparia after first being formed to reach their dark red to dark brown coloration. At room temperature the pupal stage lasted eight weeks, and at 24° C. three to four weeks. The adults lived between two to three weeks at room temperature in jars containing moist cotton wool.

When conditions in the culture jar were too wet the young stages did not survive well and few adults resulted. The following four cultures show what occurred when the *Laminaria* stipes were soft and decomposing rapidly and when the sand at the bottom of the jar became waterlogged because the excess water was not removed.

(1) Twenty eggs were laid. Of only seven larvae which matured and moved into the sand to pupate, four eventually did so and the other three died. Two adults emerged, the other two pupae died. Within two days of emerging both adults were found dead, with their wings sticking to the wet side of the jar.

(2) Thirty-one eggs were laid. Seven larvae reached their third instar. Six of these formed poorly-shaped puparia ; one died. No adults emerged.

(3) Eighty-five eggs were laid. Seventy-two living first instar larvae were found on and in the soft weed and even more may actually have been present. Thirteen eventually became third instar larvae. The dead larvae were found in a layer of water covering the sand at the bottom of the jar, on the wet inside of the jar, and on the surface of the pulpy *Laminaria* tissue. Six of the thirteen larvae pupated on the side of the jar, level with the surface of the water and covered with a thin film of it. They remained light brown or white in colour and no flies emerged. Three pupated on the side of the jar higher up and three adults emerged. The other four larvae were found dead in the water. The adults died within three days ; two were found stuck to the side of the jar and one was in the water at the bottom of the jar.

(4) Fifty-three eggs were laid. Of 11 larvae that survived, seven pupated on top of the waterlogged sand but remained light brown in colour. No flies emerged. The other four pupated near the top of the *Laminaria* stipes and eventually produced adults. Two of the adults died within six hours of emergence, another one died two days after and the last one four days after emergence.

It will be seen that the wet conditions deleteriously affected all stages except possibly the egg, all or nearly all of which hatched (culture 3). From a total of 189 eggs laid, only 38 third instar larvae were produced. Of these, eight died in that instar, 21 shortly after pupating, and the flies that emerged from the remaining nine all died within four days. As has been mentioned previously, in more normal conditions the larvae move downwards to pupate and do so in or under the sand, and it is interesting to see that while 21 larvae which went as far as was possible to attaining this situation eventually died, the nine which pupated in abnormal situations all produced adults.

In wet conditions such as these in which *Oe. buccata* suffers a great mortality, *C. frigida* survives with only slight losses, only one or two larvae occasionally being drowned.

III. The Biology of the Species

All the known species of Coelopidae occur on the sea-shore, the eggs and larvae being found in decomposing wrack beds and their pupae either among the wrack or under nearby rocks and shingle. The adults are normally closely bound to the wrack beds and their vicinity.

(1) *The Environment*

Backlund (1945*a*) divides wrack beds into three types according to size and shape, calling them wrack strings, wrack flakes and wrack banks. His definitions are altered slightly to suit the wrack beds encountered in this study.

Wrack strings are long, continuous or broken, stretches of wrack usually less than eight inches deep and twelve inches wide. They are usually found along the length of the high-tide line, and are perhaps formed only where there is a gently-rising shore extending several yards beyond the high-tide line, thus preventing the wrack from piling up. Wrack strings never become soft because they cannot retain water, and at times during dry weather their wrack may be hard and brittle.

Wrack flakes have about the same depth but are broader than wrack strings. They are formed either on fairly level parts of the shore or in shallow depressions.

Wrack banks are larger accumulations, more than eight inches deep and twelve inches wide. They are most often formed at the foot of cliffs and boulders where the wrack piles up because it cannot be pushed farther back or scattered to form strings or flakes. Wrack banks decompose rapidly and soon become very soft. Their deepest layers are always wet.

Although the three types of wrack beds approach each other in size, the physical differences and the differences in the fauna between the extreme forms—wrack strings and large wrack banks—are very distinct.

Most of the field work for this study was carried out on the wrack beds at Whitburn, Co. Durham., where the shore is conveniently divided into two parts by a concrete ramp that stretches into the sea. North of this ramp, the shore is rocky towards the sea and covered with loose rocks and pebbles more inland. There are cliffs about 30 feet high flanking the shore of this region. South of the ramp, the shore is sandy with broken stretches of shingle near the high-tide level. This southern part merges into the bay at Seaburn, which continues with a similar structure to the pier at the mouth of the River Wear. The shore in this area rises gently and there are no cliffs bordering it inland.

On the rocks north of the ramp there was always a large wrack bank at the foot of the cliffs. It measured between two to five yards long, one to three yards broad and was up to three feet deep. At times it became partly covered in rocks and shingle. A wrack string was nearly always present, parts of it on sand and parts on shingle, along the high-tide line beginning about 150 yards south of the ramp and extending into the bay at Seaburn. Both the wrack bank on the rocks and the wrack string south of the ramp can be considered " permanent " because there was nearly always some wrack in these positions. Other wrack banks were found seawards of the " permanent " one on the rocks, but they remained for only a few days at the most.

Between the positions where this wrack bank and wrack string were formed is a stretch of shore, 150 yards long, on which all three types of wrack beds were continually being formed at various intervals between the high- and low-tide levels. This region is referred to as the central region of the Whitburn shore and the wrack beds formed here remained for varying periods lasting from several hours to about three weeks. The shore rises more gradually than the rest of the Whitburn shore, and at times even contained large, shallow depressions. It was the only region where wrack flakes were formed at Whitburn.

The " permanent " wrack beds at Whitburn were largest after the high autumn equinoxial tides had cast up a great deal of wrack that had grown in the summer months. For several weeks previous to these tides large amounts could be seen floating in the bay and large temporary wrack banks were formed below the high-tide level on the shore. Eventually the wrack was cast up beyond the high-tide level and the beds formed were present throughout the winter. Additional wrack was added to them from time to time but, in general, they gradually decreased in size. By April the wrack string was dry and brittle and it remained very much in this state until the autumn.

The wrack beds at Whitburn were visited once or twice almost every week throughout the period October, 1955 to April, 1958.

Other wrack beds investigated were on the mainland opposite St. Mary's Island, Northumberland, some ten miles north of Whitburn. Here, large wrack banks, two or three feet deep, were formed at the base of some cliffs. No wrack strings or wrack flakes were ever found, and the occasional small clumps of wrack sometimes seen on the shore remained for short periods only. These wrack banks near St. Mary's Island were visited once or twice a week from September, 1955 to March, 1956, and thereafter on odd occasions until April, 1958.

All the wrack beds at Whitburn and near St. Mary's Island were composed entirely, or almost entirely, of *Laminaria* and *Fucus*. Sometimes there were small amounts

of other seaweeds present and sometimes various amounts of other organic and inorganic tidal debris.

All of the Durham coast and the Northumberland coast south of St. Mary's Island was examined at some time but no other large area of wrack beds, similar to that occurring at Whitburn, was seen.

Because of the decomposition of the wrack and the breakdown of complex organic compounds, the temperatures of the various wrack beds became higher than those of the surrounding air. When the beds were first formed, and before decomposition had taken place, the temperature was roughly the same as that of the air. After two or three days, however, when decomposition was taking place, the temperature in the wrack banks rose to as much as 17° C. above the surrounding air. The greatest increase occurred in compressed wrack, where the decomposition products could not drain away.

If the wrack banks became contaminated with sand, as those formed in the central region at Whitburn frequently did, the temperature fell to about that of the air. The sand separates the wrack, aids drainage, and absorbs heat from the decomposing wrack, all of which lowers the temperature of the banks.

Wrack strings and flakes, being shallow wrack beds lying on sand and shingle at Whitburn, were well drained and were usually about the same temperature as the surrounding air. On warm, sunny days, however, they were up to 5° C. higher than the air temperature, presumably having absorbed radiated heat.

In the following account of observations made on the species of Coelopidae in the wild, *Coelopa frigida* and *C. pilipes* are treated together; observations made on *Orygma luctuosa* and on *Oedoparea buccata* follow.

(2) *The Time and Place of Occurrence of the Adults of* C. frigida *and* C. pilipes

(a) *The Large Autumn and Winter Populations of the Flies*

At Whitburn the adults of *Coelopa frigida* and *C. pilipes* were most numerous during the autumn and winter months of the three years in which they were studied, *i.e.* after the large masses of wrack, in which their larvae feed, had been cast up on to the shore by the high equinoxial tides of September. It has previously been pointed out that the wrack beds formed at this time are larger than those formed at any other time, and this is likely to be true for other European coasts. These large autumn and winter populations are, therefore, probably a common feature in the biology of both species. Reference has already been made to this by Oldroyd (1954) in the case of *C. frigida* on the south coast of England.

(b) *Even Distribution of the Two Species in the Wrack String*

Because of the vast number of each of the two species and their secretive habits, it was impossible to estimate their total population or to observe any absolute change in their state. It was found, however, that they occurred together and were evenly distributed along the length of the wrack string and under the adjacent stones. This made it possible to calculate the percentage of each of the two flies in the total *Coelopa* population at any given time.

The flies of both species bred in large wrack banks and, as will be shown later, only a few larvae were found in the wrack string, none being present between September and March, the most important breeding period in the life of the two species. The larvae pupated on the edge of the wrack banks and under stones on its landward side. The adults emerged in large numbers and dispersed along the shore at about the high-tide level, most moving southwards of the wrack banks. That the chief direction of the dispersal is southwards may be due to some intrinsic reason, but at Whitburn this happens to be the only direction in which they can conveniently move. Any inland dispersal is limited by the cliffs and the north is barred by a

prominence. There is, moreover, often a north wind. The wrack string and central regions at Whitburn, therefore, have a population of *C. frigida* and *C. pilipes* adults that had bred in the wrack banks some few yards away. That the two species were fairly evenly distributed in these regions can be seen from Table I, which shows that the percentage of each species in the total *Coelopa* population in collections made at different parts of the wrack string differed by only small amounts.

Because of the nearness to the emerging flies, the population in the immediate vicinity of the wrack banks was liable to sudden increases, and the proportion of each of the flies in the total *Coelopa* population was not so even as that in the wrack string—nevertheless, the difference was within 20 per cent. Similar estimates for the flies actually occurring in the wrack banks were not made, as far fewer were found there than were found under the nearby stones and in the wrack string at any time ; and also because the numerous ways in which the flies could escape made it difficult to catch them.

(c) *Variations in the Percentage Composition of the Population*

On several occasions during the periods September, 1955 to March, 1956, and September, 1956 to March, 1957, between 100 and 500 adults of *Coelopa* sp. were collected from the wrack string and its immediate vicinity to discover the percentage of the total population each of the two species represented at any given time, and to observe any changes in the structure of the population. Because the wrack string and the pebbles under which the flies were found lay on sand, and because most of the

TABLE I.—*Collections of* C. frigida *and* C. pilipes *adults from different parts of the wrack string*

(*a*) From the southern half.
(*b*) From the northern half.

	C. frigida			*C. pilipes*			Percentage of *Coelopa* population	
	M.	F.	Total	M.	F.	Total	*frigida*	*pilipes*
	8.xii.55							
(*a*)	69	82	151	6	4	10	93·8	6·2
(*b*)	81	94	175	7	6	13	93·1	6·9
	30.i.56							
(*a*)	9	8	17	47	50	97	14·9	85·1
(*b*)	16	12	28	85	83	168	14·3	85·7
	16.ii.56							
(*a*)	13	20	33	111	84	195	14·5	85·5
(*b*)	8	7	15	69	63	132	10·2	89·8
	15.x.56							
(*a*)	75	38	113	25	23	48	70·2	29·8
(*b*)	41	43	84	23	14	37	69·4	30·6
	12.xi.56							
(*a*)	28	31	59	2	8	10	85·5	14·5
(*b*)	47	63	110	9	9	18	85·9	14·1
	15.xi.56							
(*a*)	29	38	67	2	1	3	95·7	4·3
(*b*)	47	72	119	3	9	12	90·8	9·2
	17.xii.56							
(*a*)	21	47	68	1	7	8	89·5	10·5
(*b*)	10	64	74	4	5	9	89·2	10·8

flies were caught during cold weather when they were lethargic, fairly large numbers could be collected with the aspirator. It should be stated that the two species of *Coelopa* cannot be distinguished when the flies are walking over wrack and sand with only their dorsal surfaces visible. Females of the two species cannot be separated with the naked eye even when closely examined; large males, however, can be distinguished. But the quick rate at which the flies were caught (on some occasions large numbers being lifted into jars by a trowel) excludes any chance of one species being selected in favour of the other. The flies caught were killed and each examined under a binocular microscope. The results of the catches for September, 1955–March 1956 appear in Table II, and those for September, 1956–March, 1957 in Table III; both sets of figures have been plotted against time in the graph (fig. 24).

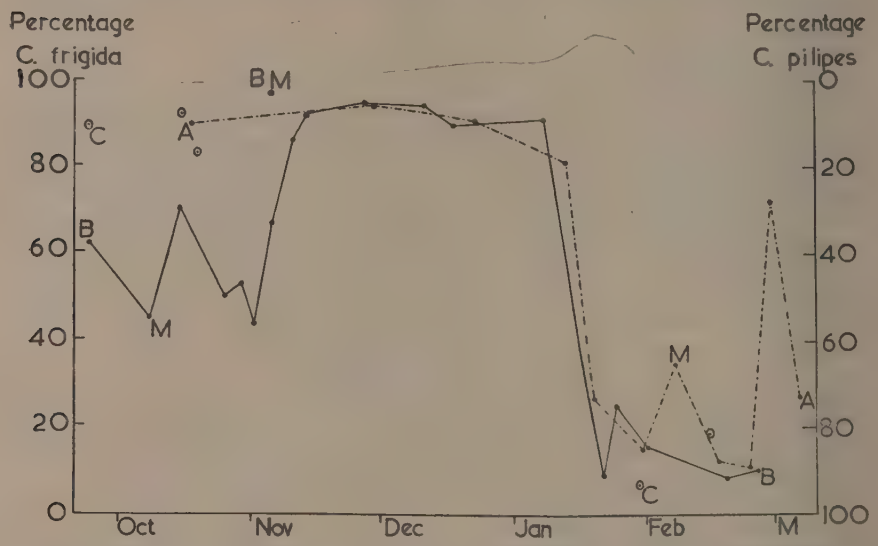


Fig. 24.—The structure of the *Coelopa* population at Whitburn. A, October, 1955, to March, 1956; B, September, 1956, to March, 1957; C, September, 1957, to March, 1958; M, migrating flies.

The tables and graph show that in October, November and December of 1955 and in November and December of 1956 over 80 per cent. of the total *Coelopa* population was *C. frigida*, but that during January of each period there was a fairly sudden swing in favour of *C. pilipes* and that before the end of the month *C. pilipes* was established at over 80 per cent. of the total population. In both periods the *Coelopa* population became greatly reduced during early March and only a few flies were found after the second week of that month. The figures for October, 1956, show that before *C. frigida* became the dominant species, the flies occurred in about equal numbers.

The fluctuations in the general trend of the curves may have been caused by mass migration phenomena such as happened on 7th February, 1956, 8th October, 1956 and particularly on 5th November, 1956, when only one species (*C. frigida*) was migrating at Whitburn, although both were present in large numbers in the wrack beds. A full account of these mass migrations will be published elsewhere.

It was decided that it was not necessary to repeat the procedure the following year, but enough flies were collected to show that the same phenomena again occurred (Table IV and graph).

TABLE II.—*The proportion of* C. frigida *and of* C. pilipes *in the total* Coelopa *population at Whitburn for October*, 1955–*March*, 1956

Date	*C. frigida* M.	F.	Total	*C. pilipes* M.	F.	Total	Percentage of *Coelopa* population *frigida*	*pilipes*
18.ix.55	34	45	79	5	4	9	89·8	10·2
28.xi.55	55	75	130	4	4	8	94·2	5·8
8.xii.55	150	176	326	13	10	23	93·4	6·6
22.xii.55	52	87	139	5	10	15	90·3	9·7
12.i.56	40	78	118	12	16	28	80·8	19·2
19.i.56	55	83	138	202	166	368	27·3	72·7
30.i.56	25	20	45	132	133	265	14·5	85·5
*7.ii.56	35	61	96	102	80	182	34·5	65·5
16.ii.56	21	27	48	180	147	327	12·8	87·2
23.ii.56	9	11	20	79	82	161	11·1	88·9
29.ii.56	50	71	121	26	18	44	73·3	26·7
6.iii.56	10	21	31	28	52	80	27·9	72·1
Totals	536	755	1291	788	722	1510		

* Migrating flies caught in flight.

TABLE III.—*The proportion of* C. frigida *and of* C. pilipes *in the total* Coelopa *population at Whitburn for September*, 1956–*February*, 1957

Date	*C. frigida* M.	F.	Total	*C. pilipes* M.	F.	Total	Percentage of *Coelopa* population *frigida*	*pilipes*
24.ix.56	27	27	54	15	18	33	62·1	37·9
*8.x.56	*a* 29	56	85	35	67	102	45·5	54·5
15.x.56	116	81	197	48	37	85	69·9	30·1
25.x.56	25	33	58	33	24	57	50·4	49·6
29.x.56	20	21	41	19	18	37	52·6	47·4
1.xi.56	6	6	12	7	9	16	42·9	57·1
5.xi.56	41	67	108	19	36	55	66·3	33·7
*5.xi.56	*a* 128, *w* 23	190, 45	386	*a* 8, *w* 0	3, 1	12	97·0	3·0
12.xi.56	75	94	169	11	17	28	85·8	14·2
15.xi.56	76	110	186	5	10	15	92·5	7·5
26.xi.56	35	64	99	3	3	6	94·3	5·7
10.xii.56	41	35	76	4	1	5	93·8	6·2
17.xii.56	31	111	142	5	12	17	89·3	10·7
7.i.57	42	117	159	7	8	15	91·4	8·6
21.i.57	24	15	39	151	223	374	9·4	90·6
24.i.57	30	67	97	124	166	290	25·1	74·9
31.i.57	11	30	41	92	126	218	15·8	84·2
18.ii.57	4	5	9	35	55	90	9·1	90·9
25.ii.57	2	10	12	43	61	104	10·3	89·7
Total flies caught	786	1184	1970	664	895	1559		

* Migrating flies caught in the air (*a*), on wrack (*w*).

It would thus seem that at Whitburn at this period of the year a *Coelopa* population in which *C. frigida* is dominant for two to three months changes rather quickly to one in which *C. pilipes* is dominant for the next two months. It is very probable that the same occurs in other areas and that it reflects some significant feature of the biology of the larvae of the two species.

TABLE IV.—*The proportion of* C. frigida *and of* C. pilipes *in the total* Coelopa *population at Whitburn for September,* 1957–*February* ,1958

Date	*C. frigida*			*C. pilipes*			Percentage of *Coelopa* population	
	M.	F.	Total	M.	F.	Total	*frigida*	*pilipes*
24.ix.57 .	41	77	118	7	8	15	88·7	11·3
16.xii.57 .	41	81	122	3	8	11	91·7	8·3
19.xii.57 .	27	43	70	10	4	14	83·3	16·7
29.i.58 .	7	4	11	72	68	140	7·3	92·7
14.ii.58 .	11	21	32	64	75	139	18·7	81·3

(d) *The Presence of only a Small Number of Flies in Spring and Summer*

From the decline in the number of flies in March of each year until the great increase in the following October few adults of either species were seen. This was mainly because far fewer individuals were actually produced, and even the small number that were produced were active because of the warmer weather and quickly dispersed. Though *C. frigida* and *C. pilipes* were scarce compared with the other species of fly present during March to October, no month in this period passed without a small number, sometimes only one or two of each, being seen.

(e) *The Places of Occurrence of the Adults*

At Whitburn during the colder months of the year, the flies of both species were usually found together in large masses under stones near the wrack beds and under wrack in the wrack string. Near St. Mary's Island at this time of year, besides the large clusters found under stones, many others were found in clefts and crannies in the clay at the base of the cliffs. The clefts could be prised open and pieces of clay broken away to reveal large numbers of the adults.

On warm days in winter the flies crawled out from under the stones and wrack and from the clefts, swarmed over the sand and wrack beds and made some short flights in the vicinity. On occasions when this occurred, the disturbance of even only a few *Laminaria* stipes revealed teeming masses of the flies. At other times when the weather was warm, the flies rested on stones and on the cliff face.

During the warmer months of the year large clusters of flies never occurred and usually only odd flies were seen either under the rocks and wrack or in flight.

Miall (1895) mentions that *C. frigida* sometimes visits flowers, and although neither this species nor *C. pilipes* have been observed on flowers near Whitburn, a few of both species have been found among grass nearby. In general, the flies seem to be restricted to the wrack beds and their immediate vicinity, but they occasionally make mass migrations.

(3) *Field Observations on the Larvae of* Coelopa frigida *and* C. pilipes

(a) *The Larvae Not Intermingling*

Before ways of distinguishing the larvae of *Coelopa frigida* and *C. pilipes* were found, collections of larvae taken together in the wrack beds were allowed to produce flies in the laboratory, and it was observed that in nearly all cases the adults resulting from any particular collection were all of one species. The only mixed collections found are given in Table V, which shows that on some occasions a few specimens of *C. pilipes* larvae were among a large number of those of *C. frigida*. In no case did a few *C. frigida* larvae occur among a mass of *C. pilipes*. Sometimes many larvae died during the attempts to obtain adults, and these could have belonged to one species only of a mixed population, the other species surviving. But collections examined after the larvae could be distinguished showed that this was not so, and

that, in general, the larvae of the two species did not occur together in the wrack beds. Of 73 collections of *Coelopa* larvae removed from the wrack beds, 54 were entirely *C. frigida*, six were chiefly *C. frigida* with a few *C. pilipes*, and 13 were entirely *C. pilipes*.

TABLE V.—*The occurrence of* C. frigida *and* C. pilipes *larvae together*

Date	Place	Flies emerging from the larvae collected	
		C. frigida	*C. pilipes*
30.xi.56	Near St. Mary's. Is.	78	1
30.xi.56	„ „ „ „	75	1
16.x .57	Whitburn central region	65	2
24.x .57	Whitburn wrack bank	84	1
10. i.57	„ „ „	100	2
16. i.57	„ „ „	42	1

(b) *Place of Occurrence of the Larvae*

Larvae of both species occurred nearly always in wrack banks and very rarely in the wrack string. On the few occasions when they were present in the string, it was deep, and really formed a small wrack bank. Table VI gives all the occasions on which larvae of *C. frigida* were found in the wrack string; *C. pilipes* larvae were never found there. *Coelopa* larvae were only rarely found in the wrack banks formed in the central region at Whitburn. These banks became contaminated with sand, which slows down the rate of decomposition and reduces the temperature.

The larvae of each of the two species were not evenly distributed within a single wrack bank, large concentrations being separated by wrack which was without or contained only a few larvae. They never occurred in the drier surface layers but were found a few inches below, in the wetter and more decomposed weed. Larvae found together were usually the same age. When mature third instar larvae were collected they successfully pupated and later produced flies without needing more wrack than that in which they had been collected. But when large numbers of younger larvae found together were collected, most of them died unless they were given additional wrack material.

On occasions, third instar larvae of *C. frigida* were found feeding in a horizontal layer, the wrack bed breaking away easily where they fed, so that a sheet of fairly dry wrack, to which only one or two larvae adhered, could be removed, exposing a white blanket of larvae on the remaining wrack. Mayhew (1939) also found them in a horizontal zone and believed that it was possibly due to their selection of an optimum temperature of about 30° C.

(c) *Vast Numbers of Larvae of* C. frigida *Together or None at All*

On three occasions when large numbers of *C. frigida* larvae were present in the wrack banks, four 2-lb. Kilner jars were each filled with larvae and wrack material from the parts of the wrack banks in which they occurred. The number of larvae, which on all three occasions were in their third instar, was found to be over 600 in each jar. These collections were only a small fraction of those actually present and at times the wrack banks at both Whitburn and near St. Mary's Island must have contained some hundreds of thousands of *C. frigida* larvae. Such vast numbers have already been alluded to by Taylor (1955), who found them on the South Devon coast.

Observations showed that the larvae of both species either occurred in large numbers in the wrack banks or were absent altogether. The females of *C. frigida* lay batches of, usually, between 60 and 90 eggs (Thompson, 1951) which hatch within

TABLE VI.—*The occurrence of* C. frigida *larvae in the wrack string*

Date	Place	Number of larvae found	Remarks
30.x.55	Whitburn central region	Several thousands	A small wrack bank in the wrack string up to 10 inches deep, 4 yards long. Had been formed for less than 10 days.
25.iv.56	Whitburn wrack string	6	In a 5-inch deep mass of compact wrack with plant debris isolated landward of wrack string. Many larvae of *Fucellia maritima* present.
30.iv.56	„	2	Similar to the preceding, but was part of main string.
3.ix.56	„	Several hundreds	Found on sand and fresh wet wrack in in open position and being fed on by sparrows. Some larvae well below H.T. level. Must have been disturbed at last H.T.
3.ix.56	„	1	In compact wrack and debris.
17.i.57	„	1	
18.ii.57	„	14	An old wrack string with plant debris, a newly formed one being present seaward of it.
16.x.57	„	237 collected, being about one-fifth of total seen	In a small wrack bank (2 feet 6 inches by 1 foot 6 inches) in the wrack string.
24.x.57	„	A collection of pupae from which emerged 84 *C. frigida* 1 *C. pilipes*	Found in an exposed position; may have been washed there by the tide.
19.xii.57	„	7	Found with a large number of *Oe. buccata* larvae.

a short time of each other, and, since the females are likely to choose fairly similar sites, a large number of larvae soon result. Thompson (1951) also found that the larvae of *C. frigida* do not survive well if only a few are present together. This is probably due to a slow rate of decomposition of the wrack, caused by only slight larval activity, with the consequence that few *Laminaria* stipes becomes suitable for feeding purposes. As mentioned in the section dealing with laboratory observations (p. 120), *Laminaria* stalk without larvae withers and dries up, but stalk on which larvae are feeding quickly decomposes, becoming very soft and pulp-like, with a brown semi-liquid running from it; there is therefore little doubt that the activity of the larvae helps greatly in the decomposition of the wrack. Thus the fact that large numbers of eggs are laid and that small groups of larvae do not survive would explain why in the wild, if present at all, the larvae were usually present in large numbers. Because wrack strings contain only small masses of loose wrack material, and because they are well drained, they decompose at a much slower rate than the wrack banks and cannot support a large population of *Coelopa* larvae. Since the alternative to a large population of larvae is apparently complete absence, this would account for their absence from the wrack strings. On the few occasions on which only a small number of larvae occurred together (Table VII), evidence was

usually found suggesting that they were survivors from a much larger mass of larvae which had been washed out of the wrack bank, or they were on wrack that had been pulled down the shore by an ebbing tide (both cases giving dispersed larvae), or else they were the remnants of the large winter population (in which case they were still found close together).

TABLE VII.—*The occurrence of only small numbers of* C. frigida *larvae in or near wrack banks*

Date	Place	Number of larvae	Remarks
27.vii.56	Among pebbles and small pieces of wrack, one yard below wrack bank on rocks at Whitburn	5	Had probably been washed out of the wrack bank (in which there were many larvae) by tide.
24.ix.56	In wet and fresh-looking wrack below H.T. level at Whitburn	28 dispersed	The 19 larvae (with 4 larvae of *Fucellia maritima*) were found about 15 yards below the 28 larvae. All had been either washed out of the wrack bed or dragged down the shore by the ebbing tide.
	In wet fragments of wrack 20 yards below H.T. level and through which a steady stream of water from higher ground was flowing	19 dispersed	
18.iii.57	Wrack bank, Whitburn rocks	18	The remains of the reduced winter population.
5.iii.58	Ditto	8	The last of the large winter population. The wrack bank, though still large (8 yards × 1–2 yards × 9–12 inches), was devoid of larvae except for these found together at the edge.
10.xii.55	Wrack bank, mainland near St. Mary's Island	11 dispersed	Survivors from a large population, found on landward edge, recent tides having almost reached this point.

(d) *Times of Occurrence of* Coelopa *Larvae*

The large numbers of larvae of *C. frigida* were first found in September of each year and continued until the following February. Numbers decreased until early March, when no more were found, although the wrack banks were still large. *C. pilipes* larvae occurred mainly from December to early March. As has been mentioned, the wrack banks are a few degrees warmer than the surrounding air and this allows the two species of *Coelopa* to breed at this time of year.

Larvae of *C. frigida* were found on a few occasions between March and the following September in each year. Times when only a small number of larvae were found appear in Tables VI and VII, and times when a fairly large number were found have been entered in Table VIII. These large numbers were found spasmodically between June and August in wrack banks formed some yards seaward of the " permanent " wrack beds in either the central region or on the rocks at Whitburn. The wrack beds formed in these positions remained for only a week to a fortnight and were continually being altered in shape and structure by the tides. Because of the high summer temperature they decomposed very rapidly, the lower layers becoming immersed in a brown semi-liquid which ran from the layers above.

TABLE VIII.—*The occurrence of large groups of larvae of* C. frigida *during March–September*

Date	Place	Remarks
6.vi.56	New wrack bank 4 yards seaward of "permanent" one at Whitburn	Vast number of large larvae which produced adults of the "*eximia*" form.
16.vii.56	New wrack bank in central region at Whitburn	A 2-lb. jar sample of wrack contained over 600 third instar larvae.
27.vii.56	Wrack bank on rocks at Whitburn	This wrack bank was 3–4 yards below the "permanent" wrack bank. Many larvae present.
20.viii.57	New wrack bank formed 20 yards below wrack string in central region	Large number of larvae present.

Larvae of either *Coelopa* species were very rarely found in the large "permanent" wrack bank on the rocks at Whitburn during March to September. During the latter part of this period, however, vast numbers of amphipods (*Orchestia gammarella*) were found there. Frequently small numbers of amphipods have been found among large groups of *Coelopa* larvae and *vice versa*, but on no occasion did large numbers of both amphipods and *Coelopa* occur together.

Thus, in each of the three years in which they were studied at Whitburn, there occurred a large autumn-winter population of *C. frigida* and *C. pilipes* larvae, followed by two to three months (mid-March to May) in which very few larvae of *C. frigida* only occurred, and this in turn was followed by a period lasting until September during which *C. frigida* bred when the right conditions and opportunities were present giving rise to spasmodic occurrences of fair numbers of larvae. Although no larvae of *C. pilipes* were found during mid-March to September, there is a possibility that groups of them may have been overlooked.

(e) *The Production of the Large* "eximia" *Form of* C. frigida

Those larvae collected on 6th June, 1956 (*see* Table VIII) pupated the following day, and five days later the flies emerged. All (51 males, 72 females) were of the large (9 mm. in male) bristly "*eximia*" form which, until Mayhew's thesis, had been thought to be a separate species.

On 14th June, 1956, 16 male and nine female adults of *C. frigida* were caught in the same wrack bed from which the larvae had been removed, and all were of the "*eximia*" form. At other times when adults of *C. frigida* have been caught and examined, less than 30 per cent were of this size and structure. Mayhew, although he had no conclusive evidence, believed that temperature had a fairly direct effect on the size of the flies, a lower temperature allowing a longer period of development and consequently giving more opportunity to feed. It is difficult to see how this could affect only a certain percentage of larvae living together in winter, and the finding of a 100 per cent. "*eximia*" population in June suggests that a low temperature is not the cause of their production. A more likely explanation is that the warmer summer temperature would quickly make available a large quantity of suitably decomposed wrack for feeding the larvae, and, since the population was less crowded than the winter ones, a greater supply of food would be available for each individual. The large larvae and consequent production of "*eximia*" type flies would then result. In laboratory conditions larvae given a superfluous supply of partially decomposed *Laminaria* nearly always produced large flies.

The large adults resulting from the wild larvae were allowed to lay eggs and the

ensuing larvae were kept in overcrowded conditions with a shortage of food. Small, less bristly flies resulted, a possibility described by Mayhew (1939).

(f) *The Ecological Separation of the Two Species*

One of the most interesting features in the biology of the Coelopidae concerns their ecology. *C. frigida* and *C. pilipes* are very similar ecologically and yet they occur together. Usually such closely related species differ in their geographical range, their habitat or their food. Gause (1934) propounded the theory that two species with similar ecology could not live together in the same area and this theory has since been supported by numerous examples (Allee *et al.* (1949) and Lack (1954) give the most important references). The converse of this theory, that two species occurring together do not have the same ecology is less easy to demonstrate. Lack (1945), however, showed that, although their range overlaps, the cormorant *Phalacrocorax carbo* and the shag *P. aristotelis* have noticeable differences in their food requirements and in their nesting habitats.

In investigating the biology of *C. frigida* and *C. pilipes*, the following differences were found in the adult stages. Firstly, although the times of occurrence of both species overlapped, *C. pilipes* were found to be more abundant from mid-January to March, whilst *C. frigida* was found chiefly from November to mid-January (p. 128). Secondly, *C. pilipes* was more prone to infection by the phoretic mite *Thinoseius fucicola* than *C. frigida*. An account of this case of phoresy will appear elsewhere. Thirdly, the two species behaved differently with regard to mass migrations and to other flight activity, a full account of which, as has already been stated, will be published elsewhere; and fourthly, females of *C. frigida* readily laid eggs in conditions in which *C. pilipes* were very reluctant to do so. These four distinctions are enough to suggest that the ecology of the two species is different, but the most significant differences in their biology should occur in the most competitive stage—the larval stage—yet no such differences were discovered.

Larvae of both species were collected from all levels in the wrack banks, from both the landward and seaward sides, from *Fucus* only, from *Laminaria* only, and from mixed wrack, and if there is a factor which separates the larvae of these two species ecologically, it is not an obvious one of food or habitat. It is possible, however, that, although the larvae of the two species ingest the same wrack material, they actually digest and absorb different components of it. A chemical analysis of the gut contents and of the excreta of the larvae of both species feeding on the same wrack material would help in solving this problem.

Mayhew (1939) suggested that *C. pilipes* larvae live in older wrack beds than *C. frigida* and this seems to be true at Whitburn, where figures given previously show that *C. pilipes* occurs after *C. frigida* in winter, although the change in the adult population is far more distinct than the corresponding change in the larval population. The theory would account for the absence of *C. pilipes* larvae during the spring and summer, when only temporary beds of fresh wrack are formed in which *C. frigida* manages to produce sporadic generations of flies.

Comparison of the anatomy of the two larvae suggests that *C. frigida*, with longer hairs on its posterior spiracles and a greater number of anterior respiratory digits, would occur in wetter and softer wrack material than *C. pilipes*. In fact, *C. pilipes* larvae, in general, occur in older and therefore more decomposed wrack, which is softer but not necessarily wetter than fresh wrack.

That some other controlling factor operates in the biology of the larvae is evident from the fact that after mid-March no larvae of either species were found in the " permanent " wrack bank at Whitburn, although at this time it was still large and contained no animals other than the nematodes and oligochaetes which are always present, and adults of *Coelopa* still occurred, though they were not so numerous as in the previous five months.

(4) *Orygma luctuosa* Meigen

(a) *The Occurrence of the Adults*

There were two periods in each of the three years occupied in this study when adults of *Orygma luctuosa* were fairly common, one in the spring, from the end of April to the end of May, and the other in autumn, throughout September. During the rest of the year the flies were scarce or entirely absent. One or two of the spring adults were still to be found in June but none was ever found in July or August, and odd flies from the autumn adults continued to be found until January but none ever occurred in February or March. *O. luctuosa* adults were not as numerous as those of *Oedoparea buccata* (p. 137) and this, combined with the fact that they were more secretive, made their emergence in April and September less noticeable than the emergence of *Oe. buccata* adults in October.

Orygma luctuosa adults were found mainly in the wrack string and in the small wrack banks, but unlike *Oe. buccata*, they were sometimes present in the large wrack banks at Whitburn and near St. Mary's Island. Normally they were never seen on the surface of the wrack string and the wrack had to be turned over to find them. When disturbed, the flies rarely took to flight, and, when they did, it was only for a few inches; they preferred to run away and make their escape under the wrack and shingle.

(b) *Field Life-history*

Eggs were very difficult to find and very few were seen in the large amount of wrack material collected and examined a few days after the emergence of the adults in April and September. Those that were seen had been laid singly, but a number were together in a small area inside soft weed, with their two filaments either lying along its surface or sticking into the air.

The larvae fed on wrack more decomposed than that used by *Oe. buccata* and they were usually found among a well-compressed mixture of mainly *Fucus* and *Laminaria*, with small amounts of other seaweeds. They occurred mainly in small wrack banks in the central region of the Whitburn shore, but odd specimens were found in the wrack string and in the large wrack bank. Only small groups of up to about 25 larvae occurred together, and single ones were often found; no masses of larvae like those occurring in *C. pilipes* and *C. frigida*, or even like the much smaller ones occurring in *Oe. buccata* were found. Most mature larvae were found in May, September and October, but a few were found in November and December.

Orygma luctuosa was the only species of the four Coelopidae studied that always pupated within the wrack bed itself. The larvae worked their way into pieces of tightly compressed wrack and, since they contracted in forming the puparia, the latter were usually found free in a small chamber in the wrack material.

(c) *The Number of Flies Present*

The adults appeared to be evenly distributed along the length of the wrack string and small wrack banks, so that, if the total number of flies occurring in a known fraction of the wrack material was known, the size of the total population present could be estimated. During one of the periods (September, 1956) when the fly was most common, the wrack string and small wrack banks contained about 165 yards of wrack, and in addition there were smaller strings of wrack, inland to the main one, measuring together 40 yards, giving a total of 205 yards of wrack material. In May, 1957, there were 200 yards of wrack material. On seven occasions during these periods an attempt was made to catch with an aspirator all the flies occurring in and under five stretches of wrack each 4 yards long, in order to calculate the total

size of the population. The decrease in the population in the spring of 1957 was then examined by catching all the *Orygma luctuosa* flies possible in one hour on seven subsequent occasions. Only a few flies escaped, one or two being lost through their disappearing among the wrack and shingle or by taking to flight. The total number of flies present in the population at any given time (Table IX) has been estimated on the assumption that 20 per cent. escaped, although fewer were actually seen to do so.

The number of flies caught on four occasions in each of the two populations examined are close enough (20–25 for September, 1956 ; 28–46 for April–May, 1957) to show that they are a fair basis for estimating the total population present. Although the size of neither the spring 1956 nor the autumn 1957 populations were calculated, they both were noticeably less than the two populations that were studied. It is probable that the maximum total population of *Orygma luctuosa* adults that occurred on the Whitburn shore at any one time during the periods of greatest abundance never exceeded seven or eight hundred. This is about one-quarter of that estimated for *Oedoparea buccata* (p. 139) and agrees well with the impression gained when working among them in the field. From the figures given for the population of spring 1957, it can be seen that within five weeks of the emergence of the flies, the population was reduced to only a few, and since in the laboratory adults live for two to four weeks at the most, less than twice this number, *i.e.* fourteen to sixteen hundred, were produced in each of the two seasons of each year.

TABLE IX.—*The size of the* Orygma luctuosa *population at Whitburn*

Date	Number of flies caught M.	F.	Total	Length of wrack string in yards	Fraction examined	Estimated total population allowing 20 per cent. escape
10.ix.56 .	10	10	20	205	1/10	250
20.ix.56 .	17	4	21	205	1/10	260
24.ix.56 .	16	5	21	205	1/10	260
27.ix.56 .	20	5	25	205	1/10	310
30.iv.57 .	13	15	28	200	1/10	350
3.v.57 .	24	12	36	200	1/10	450
8.v.57 .	37	9	46	200	1/10 in 1 hour	570
13.v.57 .	19	12	31	.	,,	390
21.v.57 .	5	8	13	.	,,	160
28.v.57 .	4	2	6	.	,,	75
6.vi.57 .	0	1	1	.	,,	Few.
11.vi.57 .	2	1	3	.	,,	Few.
13.vi.57 .	0	0	0	.	,,	Absent.

(5) *Oedoparea buccata* (Fallén)

(a) *The Occurrence of the Adults*

The adults of *Oedoparea buccata* began to emerge at Whitburn in the second week of October in each of the three years in which they were studied, and they became very common within a few days. They were continually found in large numbers from then until the second week in December in 1955, and until the third week in January in both 1957 and 1958. Then followed a rapid decrease from abundance to either extreme scarcity or complete absence, and this state remained until the emergence of fresh flies in the following October. During this period in 1956, one or two flies were found on occasions until April, but during the same period in 1957, the only flies found were some very small specimens in May. The flies never occurred in June, July or August in either of these years.

The adults were found in the wrack string only and never occurred in the larger masses. If the clumps of *Laminaria* stalks which made up the wrack string were gently turned over, the flies could be seen walking among the weed and over the ground below, and after a few seconds some of them would take to flight, settling again a few yards farther along the wrack or on the sand nearby. The adults were rarely seen to fly except when they were disturbed.

During the three to four months in which the adults were about there were two to four generations of the fly.

(b) *Field Life-history*

Shortly after the sudden emergence of the adults in October and until December of each of the years 1956 and 1957, eggs were found, after assiduous search, on the *Laminaria* stipes in the wrack string. The *Laminaria* stipes at this time had been freshly cast up on the shore, were firm and covered in a mucilaginous secretion. The eggs were laid in groups on the surface of the stipes, on fronds and among epiphytes growing on them.

The larvae fed on the outside of the wet, but well-drained *Laminaria* stipes and fronds, making inroads into the more central tissue ; the stipes thus came sometimes to have a corrugated appearance, but with decomposition it soon became softer and lost this appearance. Larvae of *Oe. buccata* were never found in *Fucus*. Because of the rather exposed position in which the larvae fed and the continual risk of the wrack string drying out, they were found only among the deep stipes of the wrack string which were often partly buried in damp sand. The larvae were present in isolated unevenly distributed groups along the whole length of the wrack string, the groups each containing between 30 and 300 larvae. What looked like suitable habitats between the groups were devoid of larvae. They occurred in the wrack string only and never in the larger wrack beds at Whitburn, nor did they ever occur near St. Mary's Island, where only wrack banks are formed.

Wrack strings being thin, shallow beds of wrack, they are soon used up as a supply of food, and as the *Laminaria* dries up quickly, it soon becomes hard and withered and therefore unsuitable as food for the larvae of *Oe. buccata*. In 1957 this state was reached in the second week of February, the last larvae of *Oe. buccata* being found on the 11th of that month. In 1956 and 1958, however, the wrack string was still suitable April and until larvae continued to be present until mid-March. It would thus seem that the length of time larvae can exist is determined primarily by the availability of food and not by the climate, although, of course, climate is one of the chief factors which determine the size of the wrack string and is constantly affecting it. The short period for the larval stages in the winter of 1956–57 may in some way account for the production of the very small specimens of *Oe. buccata* adults which were found in the following May.

The orange-brown puparia of *Oe. buccata* were found close together, but not touching or adhering as in *Coelopa frigida*, in the top layers of sand under the wrack string or under adjacent stones on its landward side.

The pupae which resulted from larvae occurring in January to March eventually gave rise to adults in the following October.

(c) *The Size of the Population*

The adults appeared to be evenly distributed along the whole length of the wrack string and the total number of flies was calculated in the same way as that described for *Orygma luctuosa*. During the period in which the fly was common, in December, 1955, the wrack string contained about 165 yards of wrack, and in addition there were smaller strings, inland to the main one, measuring together 65 yards, giving a total of 230 yards of wrack material. In November, 1956, there were 220 yards and in

December, 1957, 270 yards of wrack material. On seven occasions when the fly was common, five stretches of wrack, each three yards long and separated by about 30 yards, were examined and an attempt made to catch all the *Oe. buccata* adults occurring in them. The amount of wrack disturbed was thus between one-fourteenth and one-eighteenth of the total amount present in the wrack string. The depth and width of wrack varied so little along the length as not to need consideration.

The results of the investigation appear in Table X.

TABLE X.—*An estimation of the size of the* Oe. buccata *population when at its maximum*

Date	Number of flies caught M.	F.	Total	Length of wrack string in yards	Fraction examined	Estimated total population assuming one-third escaped
8.xii.55 .	26	24	50	230	1/15	1100
1.xi.56 .	64	7	71	220	1/15	1600
12.xi.56 .	53	28	81	220	1/15	1800
15.xi.56 .	46	19	65	220	1/15	1500
20.i.57 .	41	21	62	210	1/14	1300
16.xii.57 .	24	14	38	270	1/18	1000
19.xii.57 .	37	7	44	270	1/18	1200

It is difficult to estimate the number of flies that escaped capture—some, of course, were seen to do so, usually by taking flight, and no doubt there were a few not seen to escape. In the last column of the table the size of the population has been calculated, assuming that one-third of the flies in the stretches of wrack examined escaped. Since it is certain fewer than this actually did escape, the figures given represent outside estimates of the number of flies present.

The figures for each of the three seasons do not vary to a great extent; there are therefore, probably between 1000 and 2000 flies present at any one time between the emergence in October and their decrease nine to fourteen weeks later. During this time there are two to four generations of the fly, so there are probably not more than 8000 individuals produced in a season.

Table XI, giving the numbers of flies caught during the decrease in the size of the population in the two years this was studied, shows that these fall from their height to zero within about two weeks. Because of the smaller numbers of flies present, a greater amount of wrack was examined in order that a more accurate estimate could be made.

TABLE XI.—*The decrease in the population of* Oe. buccata

Date	Number of flies caught M.	F.	Total	Length of wrack string in yards	Fraction examined	Estimated total population assuming one-third escaped
8.xii.55 .	26	24	50	230	1/15	1100
15.xii.55 .	8	2	10	230	1/15	225
18.xii.55 .	3	1	4	230	1/10	60
22.xii.55 .	0	0	0	230	1/4	0
20.i.57 .	41	21	62	210	1/14	1300
24.i.57 .	16	12	28	Wrack string	1/14	600
27.i.57 .	4	3	7	drying out	1/14	150
31.i.57 .	2	2	4	but length	1/4	25
4.ii.57 .	0	0	0	about same	1/4	0

Summary

The systematics, life-history and biology of four species of Coelopidae—*Coelopa frigida* (Fabricius), *C. pilipes* Haliday, *Orygma luctuosa* Meigen and *Oedoparea buccata* (Fallén) are discussed.

The third instar larva and puparium of *C. frigida* are described and features in which those of *C. pilipes* differ from them are discussed. The egg, larval instars and puparium of both *O. luctuosa* and *Oe. buccata* are described and figured. Remarks on the systematic position of *Oe. buccata* are included.

An account of the methods of keeping cultures of each of the four species and observations made on their life-histories in the laboratory are given.

The wrack beds in which the four species live and breed are described. Some problems in the ecology of *C. frigida* and *C. pilipes*, including their ecological separation, are discussed and an account is given of the field life-histories of *O. luctuosa* and *Oe. buccata*.

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